

## UPLAND BIRD COMMUNITIES ON SANTO, VANUATU, SOUTHWEST PACIFIC

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**ABSTRACT.**—We surveyed indigenous landbirds at two upland, mostly forested sites in southwestern Santo, Vanuatu. One site (Wunaroahare, 600–1,250 m elevation) lies on the western, rain-shadowed slope of Mt. Tabwemasana. The other (Tsaraepae, 500–700 m elevation) is 16 km to the south, on the southeastern, very wet slope of Peak Santo. These are the richest single-site bird communities yet surveyed in Vanuatu, with 30 species of resident birds recorded at each site, 27 of which were common to both sites, including 6 species endemic to Vanuatu. We judged that 12 of the shared species were common at both sites. The non-overlapping species were a megapode, a parrot, and four understory passerines. We present new data on vocalizations for four species endemic to Vanuatu (*Ptilinopus tannensis*, *Todiramphus farquhari*, *Neolalage banksiana*) or to Vanuatu plus New Caledonia (*Clytorhynchus pachycephaloides*). We found less seasonality in breeding than previously reported for Vanuatu. Most human impact at the sites today may be from non-native mammals (rats, cats, pigs, cows), along with low levels of hunting and forest clearing. Based on prehistoric bones from elsewhere in Vanuatu, we suspect that formerly the sites on Santo may have supported additional species of megapode, hawk, parrot, and starling. Received 28 July 2005, accepted 14 March 2006.

The Republic of Vanuatu (12,195 km<sup>2</sup>; Fig. 1) consists of 12 islands >270 km<sup>2</sup> and nearly 100 smaller ones in the tropical Pacific Ocean. Approximately 190,000 persons inhabit 70 islands (Lal and Fortune 2000) that range from active volcanoes to limestone islands to older, geologically composite islands, such as Santo (MacFarlane et al. 1988, Nunn 1994). Analyses of avian distributions in Vanuatu, based largely on collections made during the Whitney South Sea Expedition on 31 islands in 1926 and 1927 (e.g., Mayr 1934, 1941), have been important in the development of evolutionary theory (Mayr 1963) and the fields of island biogeography (MacArthur and Wilson 1967) and community ecology (Diamond 1975). Aside from the study by Scott (1946), field ornithology in Vanuatu lagged until the Percy Sladen expedition of 1971 focused on inter-island and altitudinal patterns of avian distribution across six islands in the archipelago (Medway and Marshall 1975). Despite the continued interest by ecologists in the results

of surveys conducted decades ago (e.g., Sanderson et al. 1998, Gotelli and Entsminger 2001), little recent attention has been paid to gathering new data on intra- and inter-island variation in Vanuatu's bird communities (although see Bowen 1997). Bregulla (1992) summarized information on identification, life-history, and distribution for each species recorded from the island group, yet made it clear that much remains to be learned about the basic biology of Vanuatu's birds. Although most biogeographic analyses of insular faunas (or floras) are based on lists of species from an entire island, such lists typically contain species that seldom, if ever, interact because they are not syntopic. Especially on large islands such as Santo, the sets of species found at single sites provide fertile grounds for analysis.

In 2002 and 2003, we made two trips to Santo, Vanuatu's largest (3,900 km<sup>2</sup>) and highest (1,879 m) island, home to eight of the nine bird species endemic to the archipelago (Bregulla 1992). We surveyed birds at two mid-elevation rainforest sites, one each on the southeastern (windward) and western (leeward) slopes of Santo's rugged west-coast mountain range. Our surveys were based on sight/sound records, mist netting, tape-recordings, and specimens collected: skins with wings spread, skeletons, tissues, stomach contents, and ectoparasites from the same indi-

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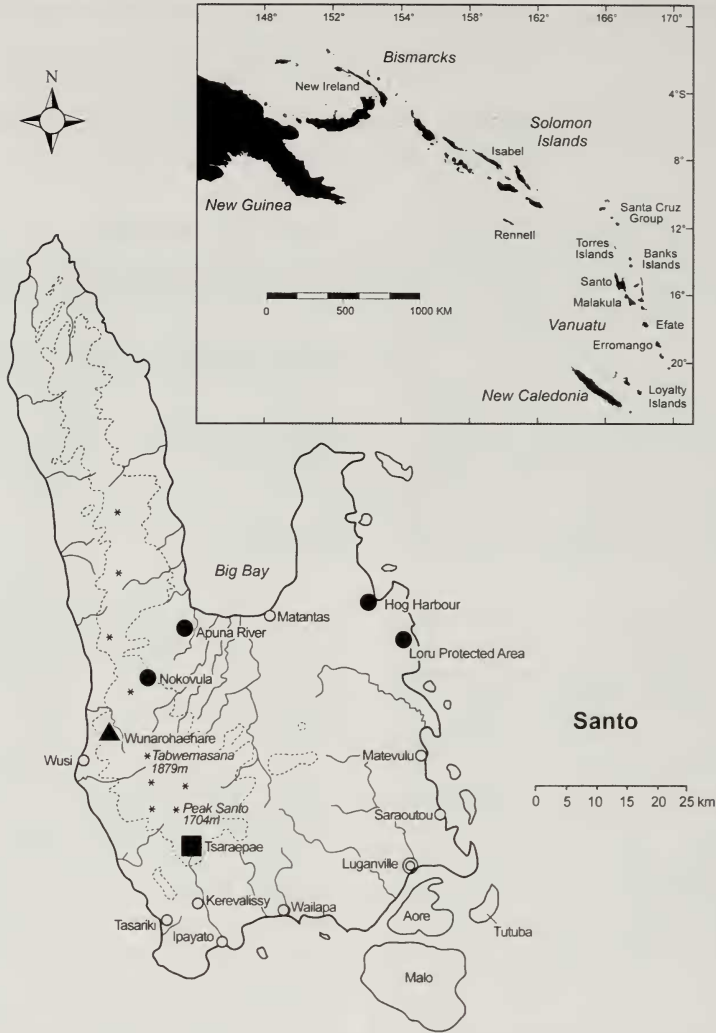


FIG. 1. Map of Espiritu Santo, Vanuatu, with an inset of Melanesia. Islands and island groups mentioned in the text are named. Sites of bird surveys conducted from 2002–2003 by the authors are indicated by the triangle (Wunaroahachare) and the square (Tsaraepae), and filled circles indicate sites surveyed by Bowen (1997; Loru Protected Area) and Medway and Marshall (1975; Nokovula, Apuna River, Hog Harbour). Asterisks = mountain peaks >1,400 m; dashed line = 600-m contour.

vidual, along with data on habitat, molt, diet, and reproductive condition. Such information is a first step in the investigation of ecological, morphological, and genetic differences among populations, and it is important for conservation efforts that often focus on endemic taxa.

In this paper, we present the results of our surveys at each site, focusing on Vanuatu's endemic and poorly known species. We also present comparisons with previous surveys at sites elsewhere on Santo and in the Solomon Islands.

METHODS

The island of Espiritu Santo (generally called Santo; Fig. 1) probably originated in the Oligocene (ca. 25–30 mya) through volcanism and tectonic uplift, although most of its land formed during or since the Miocene through these same processes (Mallick 1975, Collot and Fisher 1989). Much of the island's eastern half is flat or has rolling hills, with most land <300 m in elevation and very little of it above 600 m. The western half of Santo is dominated by a north-south trending moun-

TABLE 1. Study sites and mist-netting effort on Santo, Vanuatu, 2002–2003.

Site (latitude, longitude)	Major habitats	Netting dates	Elevation (m)	No. nets	Net-hr
Wusi village (15° 22.7' S, 166° 39.7' E)	Dry lowland forest, secondary scrub	22–27 Oct 2002, 4–5 Nov 2002	0–50	8	165
Wunaroahachare <sup>a</sup> (15° 20.5' S, 166° 40.5' E)	Humid premontane forest, forest patches, grassy ridge	29 Oct–2 Nov 2002	600–1200	18	337
Kerevalissy village (15° 35.7' S, 166° 50.0' E)	Secondary lowland forest patches	3–6 and 14 Jun 2003	200	5	14
Tsaraepae <sup>a</sup> (15° 32.7' S, 166° 48.4' E)	Wet, primary, premontane forest	7–14 Jun 2003	500–700	15	575

<sup>a</sup> Primary study sites.

tain range that reaches its greatest height at Mt. Tabwemasana (1,879 m). Prevailing winds push moist air off the Pacific Ocean across the eastern lowlands and into the east- or southeast-facing slopes of the main cordillera. Thus, the eastern and southern slopes of the cordillera are humid with high precipitation, whereas the western slopes, which plunge into the Pacific with little development of a coastal plain, lie in a rain shadow and are relatively dry.

From 22 October to 5 November 2002, we (AWK, JJK) mist-netted and observed birds in dry forest and scrub in the vicinity of Wusi (Fig. 1, Table 1), a village in the rain shadow on the western coast 10 km west of Mt. Tabwemasana, and in humid premontane forests and grassy ridges from 600 to 1,250 m elevation on the northern slope of Mt. Wunaroahachare (denoted by a triangle in Fig. 1; Table 1). At Wunaroahachare, figs (*Ficus* spp.) and nutmegs (*Myristica* spp.) are the dominant fruiting trees. Tree ferns (*Cyathea* spp., *Dicksonia* spp.) become common above 700 m in a transitional habitat between the “high-stature lowland rain forest” and the “montane cloud forest” (described in Mueller-Dombois and Fosberg 1998). The weather at Wunaroahachare is cool and moist in the morning, as cloud cover descends below 600 m. By 10:00 UTC + 11, however, the clouds dissipate and the canopy receives direct sunlight. Short periods (<1 hr) of rain occur most afternoons.

From 3 to 14 June 2003, AWK, JJK, and DWS worked on the southern slopes of Peak Santo (also called Lairiri; 1,704 m), ~16 km south-southeast of Mt. Tabwemasana. This area received the full precipitative effects of moist air coming off the Pacific, and was

much wetter than sites in the rain shadow—Wusi and Wunaroahachare. From 3 to 7 June, we surveyed a patchy secondary forest near Kerevalissy village (Fig. 1, Table 1), a landscape dominated by coconut plantations, ~4 km north of the coastal village of Ipayato. From 7 to 14 June, we mist-netted (Table 1) and observed birds on the southern slopes of Peak Santo at Tsaraepae (~500 m; denoted by the square in Fig. 1) and on nearby slopes up to 700 m elevation. Ridges in the lower elevations had a broken canopy and were cleared of undergrowth, grazed by feral cattle (*Bos taurus*), and browsed by feral pigs (*Sus scrofa*). The area >700 m was mainly tall (canopy 12–25 m) forest.

Trees identified (by DWS) to genus included *Garuga* (Burseraceae), *Calophyllum* (Clusiaceae), *Elaeocarpus* (Elaeocarpaceae), *Hernandia* (Hernandiaceae), *Ficus* (Moraceae; at least five species, some of them emergent), and *Myristica* (Myristicaceae); those we identified to species included *Barringtonia edulis* (Barringtoniaceae) and *Endospermum medullosum* (Euphorbiaceae; often emergent). There also were a number of unknown species, including various Myrtaceae and Rubiaceae. Also present were *Pandanus* spp. (Pandanaaceae), tree-ferns (*Cyathea* spp.; Cyatheaceae), and *Dicksonia* spp. (Dicksoniaceae). The edges included trees and shrubs of *Macaranga* spp. (Euphorbiaceae), *Incarpus fagifer* (Fabaceae), *Ficus* spp., *Piper* spp. (Piperaceae), *Alphitonia* spp. (Rhamnaceae), *Pipturus* spp. (Urticaceae), palms (*Cocos* spp.; *Metroxylon* spp. [Arecaceae]), and thickets of *Hibiscus tiliaceus* (Malvaceae), bananas (Musaceae), and ginger (Zingiberaceae).

The weather at Kerevalissy and Tsaraepae

in 2003 was extremely wet, with heavy rainfall occurring on 11 of our 12 days. On 9 days we estimated that the daily rainfall exceeded 100 mm, including 6 days (5, 6, 8, 9, 12, and 13 June) on which it probably exceeded 150 mm. The excessive rain was due to an unusually late tropical storm that paused just north of Santo over the Banks and Torres islands. Because avian activity did not diminish noticeably during rains at Tsaraepae, we conducted our sight/sound surveys and set mist nets even during the very rainy weather. Vocalizations were tape-recorded on several days at each of our two primary sites (Table 1), and the original tapes were deposited in the Florida Museum of Natural History (UF) Sound Archives. Birds were collected according to the stipulations of our permits from the Vanuatu Ministry of Lands, Environment Unit. Specimens were prepared as various combinations of round skins, complete or partial skeletons, and with spread wings. Stomach contents and two tissue samples were taken from each specimen; one tissue sample is housed at UF and the other at the Louisiana State University Museum of Natural Science. All non-tissue material is housed at UF. As far as we know, neither tissue nor skeletal specimens of birds had been collected previously in Vanuatu. The skeletal specimens of the Vanuatu endemics *Ducula bakeri*, *Ptilinopus tannensis*, *Todiramphus farquhari*, *Neolalage banksiana*, *Zosterops flavifrons*, and *Glyciphobia notabilis* (see Tables 2 and 3 for English common names) are the first in the world's inventories.

In addition to our work at the two primary sites, JJK and AWK collected and surveyed birds in patchy forested sites near sea level on the eastern coast of Santo for 2 days in October–November 2002 and for 4 days in June 2003. In northern Santo, AWK visited lowland forests of the Vatte Conservation Area (near Matantas; Fig. 1) from 17 to 19 November 2002. DWS visited Aore Island (Fig. 1) on 15–16 June 2003, surveying (sight/sound only) birds in patches of tall (canopy 15–30 m) lowland rainforest.

Although this was the first visit to Santo by all three authors, AWK and especially DWS have wide experience with the avifauna in western Oceania. They know the vocalizations and behaviors of all but one of the genera

found on Santo. Nonetheless, cryptic species may have been missed if they were not vocal during our visits.

## RESULTS

*Diversity and community composition.*—We recorded 33 indigenous species of landbirds at Wunaroahare and Tsaraepae, with 27 species common to both sites (Table 2). As is the case across most of Oceania (Steadman 1997, 2006b), pigeons and doves (Columbidae) composed a large part of the avifauna; the same seven species of columbids were found at each site. We also recorded seven of the eight species endemic to Vanuatu, failing to record only *Aplonis santovestris* (see below). Six of the endemic species (all but *Megapodius layardi*) were recorded at both sites.

Although three species of non-native birds are widespread on Santo (Red Junglefowl, *Gallus gallus*; Common Myna, *Acridotheres tristis*; and Black-headed Munia, *Lonchura malacca*), the only one we recorded was *G. gallus*, and it was uncommon (<5/day) at both sites. All three species were common in plantations and villages at elevations lower than those of Wunaroahare and Tsaraepae. Contamination of the bird communities by non-native species on Santo is minor (by Pacific Island standards); however, both sites are heavily infested with non-native mammals. At Tsaraepae, we noted feral cats (*Felis catus*), pigs (*Sus scrofa*), and cows (*Bos taurus*); dogs (*Canis familiaris*) seemed to be confined to villages. Inside our leaf house at Tsaraepae, DWS snap-trapped 10 rats (7 *Rattus rattus*, 3 *R. exulans*) in 3 nights, using only two traps.

Although species richness was the same at our two primary sites, composition of the landbird communities differed slightly. *Megapodius layardi*, *Charmosyna palmarum*, and *Clytorhynchus pachycephaloides* were found only at Tsaraepae, although the latter species was found in the dry forests near Wusi (lower elevations than at Wunaroahare). The mound-building *Megapodius layardi* may be absent from dry forests due to unsuitable soil conditions. Our failure to record *Charmosyna palmarum* at Wunaroahare may have been a consequence of its nomadic habits (see *C. palmarum* species account, below). Three species with widespread distributions in Oceania—*Lalage leucopyga*, *Turdus polioce-*



*phalus*, and *Petroica multicolor*—were not recorded at Tsaraepae. The four passerine species found at only one of the two sites have been recorded on both sides of the cordillera (Medway and Marshall 1975; Table 3), so their apparent absence at one site may be related to inadequate sampling. We note, however, that our guides at Tsaraepae did not recognize the illustration in Bregulla (1992) of *Turdus poliocephalus*, suggesting that the local absence of this conspicuous species was genuine. The guides did not distinguish between *L. maculosa* and *L. leucopyga* (Hakei language names for *Lalage* were “vasoimoto” and “losoloso,” which seemed to apply to either species), so it is possible that the latter species was present. Our guides did know *Petroica multicolor*, however, and called it “panopano.”

We observed inter-site differences in the altitudinal ranges of some species. Two endemic species characteristic of the highlands (*Ducula bakeri* and *Glycyfobia notabilis*) were more common at Tsaraepae than at Wunaroahare, where *D. bakeri* was not seen below 800 m. At Tsaraepae, *D. bakeri* was found regularly as low as 500 m and locally in forest patches as low as 200 m along the trail south toward the coast. At Tsaraepae, the fantail, *Rhipidura spilodera*, was scarce above 500 m, but at Wunaroahare it was common up to 800 m. Some species associated with less forested habitats (*Todiramphus chloris*, *Lalage maculosa*, *Gerygone flavolateralis*) were found at higher elevations at Wunaroahare, where we sampled open habitats up to 1,000+ m; at Tsaraepae, however, we did not find these species at elevations above 550 m, which were almost entirely forested.

*Seasonality of reproduction.*—Our visit to Wunaroahare during October–November coincided with the reported breeding period for most species of birds in Vanuatu, which generally is September–February (Bregulla 1992). Our visit to Tsaraepae took place during June, a month when Bregulla (1992) found breeding activity for only 5 of the 33 species we recorded (Table 2). We found less evidence of marked seasonality in breeding, with signs of reproductive activity (enlarged gonads in specimens, active nests, or recently fledged juveniles) in 20 of 23 species at Wunaroahare and 12 of 20 species at Tsaraepae

(Table 4). We suspect, nevertheless, that the difference between the two sites (87% versus 60% of species) does reflect seasonal trends more than inter-site variation.

#### Selected Species Accounts

We present our findings for species endemic to Vanuatu and for some others that are poorly known in Vanuatu or throughout their range.

*Megapodius layardi.*—The endemic Vanuatu Megapode was not recorded at Wunaroahare, but, at Tsaraepae on 11 and 12 June, three individuals were heard calling at an elevation of 550 m in the thick undergrowth near an active incubation mound in a large tract of forest. This was the only mound near Tsaraepae known to our guides. Another bird was observed in a dense *Hibiscus tiliaceus* thicket at 600 m on 11 June. Single birds also were seen twice in secondary forest patches on Santo’s eastern coast, and once near Matantas. Villagers showed us eggs from an active mound near Matevulu on 16 June.

*Chalcophaps indica.*—This terrestrial dove is widespread in Oceania, with the subspecies *C. i. sandwichensis* confined to New Caledonia, the Santa Cruz Group, and Vanuatu. Abundant in disturbed forest and forest edge from sea level to 400 m elevation (lower than either study site), the Emerald Dove was much less common in more mature forest near our two primary study sites. In 337 net-hr at Wunaroahare, only one bird was netted at elevations >500 m, whereas five were netted in 165 net-hr at 0–50 m near Wusi. Because it seldom vocalizes and is rather furtive, mist-netting may yield better evidence of the Emerald Dove’s population density than auditory or visual data. The species is common in village gardens, where it often is lured with papaya (*Carica papaya*) into traps; stomachs of nearly all collected individuals contained seeds of this non-native plant. The four birds taken near Wusi village included two males with enlarged testes, an adult male (no bursa) with unenlarged testes, and an adult female (no bursa, convoluted oviduct) with slightly enlarged ova. The single bird from Tsaraepae was a male with enlarged testes.

*Ptilinopus tannensis.*—Endemic to Vanuatu, the Tanna Fruit Dove was common (up to 15 per day) at each site, especially in montane forests. This fruit dove was heard much more

TABLE 2. Summary of native bird communities at two sites (Wunaroahare, 600–1,200 m; Tsaraepae, 500–700 m) on Santo, Vanuatu, surveyed in 2002–2003. E = endemic to Vanuatu, e = endemic to Vanuatu plus New Caledonia and/or the Santa Cruz Group. Relative abundance: c = common (encountered regularly by all observers), u = uncommon (encountered daily or almost daily in small numbers), r = rare (encountered fewer than five times), — = not recorded. Foraging guild (microhabitat/prey): A = aerial, C = canopy, T = terrestrial, U = understory, F = fruit, G = granivore (seeds), I = insects and other invertebrates, N = nectar, V = vertebrates. Avian nomenclature follows Dickinson (2003), except that we do not recognize *Aerodramus*, which has been used for some species in *Collocalia* (but see Price et al. 2004).

Species	Relative abundance		Foraging guild
	Wunaroahare	Tsaraepae	
<b>Megapodiidae</b>			
<i>Megapodius layardi</i> , Vanuatu Megapode (E)	—	r	T/FG,I
<b>Accipitridae</b>			
<i>Circus approximans</i> , Swamp Harrier	r	r	A/V
<b>Columbidae</b>			
<i>Columba vitiensis leopoldi</i> , White-throated Pigeon	r	u	T,U,C/FG
<i>Macropygia m. mackinlayi</i> , Mackinlay's Cuckoo-Dove	c	u	U/F
<i>Chalcophaps indica sandwichensis</i> , Emerald Dove	c	c	T/G,I,F
<i>Ptilinopus tannensis</i> , Tanna Fruit Dove (E)	c	c	C/F
<i>Ptilinopus greyii</i> , Red-bellied Fruit Dove (e)	c	c	U,C/F
<i>Ducula p. pacifica</i> , Pacific Imperial Pigeon	c	c	C/F
<i>Ducula bakeri</i> , Vanuatu Imperial Pigeon (E)	u	c	C/F
<b>Psittacidae</b>			
<i>Trichoglossus haematodus massena</i> , Rainbow Lorikeet	c	c	C/N,F
<i>Charmosyna palmarum</i> , Palm Lorikeet (e)	—	r	C/N
<b>Cuculidae</b>			
<i>Chrysococcyx lucidus layardi</i> , Shining Bronze-Cuckoo	u	r	C/I?
<b>Apodidae</b>			
<i>Collocalia esculenta uropygialis</i> , Glossy Swiftlet	c	c	A/I
<i>Collocalia v. vanikorensis</i> , Uniform Swiftlet	c	c	A/I
<b>Alcedinidae</b>			
<i>Todiramphus farquhari</i> , Chestnut-bellied Kingfisher (E)	u	c	U/I,V
<i>Todiramphus chloris santoensis</i> , Collared Kingfisher	u	u	C/I,V
<b>Meliphagidae</b>			
<i>Glycifolia n. notabilis</i> , White-bellied Honeyeater (E)	u	u	C/N,I
<i>Myzomela cardinalis tenuis</i> , Cardinal Honeyeater	c	c	C/N,I
<b>Acanthizidae</b>			
<i>Gerygone flավolateralis correiaae</i> , Fan-tailed Gerygone	u	u	U,C/I
<b>Artamidae</b>			
<i>Artamus leucorhynchus tenuis</i> , White-breasted Woodswallow	u	u	A/I
<b>Campephagidae</b>			
<i>Coracina caledonica thilenii</i> , Melanesian Cuckoo-shrike	u	u	U,C/F,I
<i>Lalage maculosa modesta</i> , Polynesian Triller	u	r	U,C/F,I
<i>Lalage leucopyga albiloris</i> , Long-tailed Triller	u	—	U/F,I
<b>Pachycephalidae</b>			
<i>Pachycephala [pectoralis] caledonica intacta</i> , New Caledonian Whistler (e)	c	c	U/I
<b>Petroicidae</b>			
<i>Petroica multicolor ambrynensis</i> , Pacific Robin	u	—	U,C/F,I
<b>Rhipiduridae</b>			
<i>Rhipidura [fuliginosa] albiscapa brenchleyi</i> , Gray Fantail	r	u	U/I
<i>Rhipidura s. spilodera</i> , Streaked Fantail	c	u	T,U/I

TABLE 2. Continued.

Species	Relative abundance		Foraging guild
	Wunaroahare	Tsaraepae	
<b>Monarchidae</b>			
<i>Neolalage banksiana</i> , Buff-bellied Monarch (E)	c	c	U/I
<i>Clytorhynchus pachycephaloides griseescens</i> , Southern Shrikebill (e)	—	u	U/I
<i>Myiagra caledonica marinae</i> , Melanesian Flycatcher	c	c	U,C/I
<b>Zosteropidae</b>			
<i>Zosterops flavifrons brevicauda</i> , Yellow-fronted White-eye (E)	c	c	U,C/N,FI
<i>Zosterops lateralis tropicus</i> , Silver-eye	c	c	U,C/N,FI
<b>Turdidae</b>			
<i>Turdus poliocephalus vanikorensis</i> , Island Thrush	c	—	T,U/FI

often than seen, although it called less frequently than the Red-bellied Fruit Dove. Contrary to Medway and Marshall (1975) and Bowen (1997), we found the Tanna Fruit Dove above 500 m; it remained common up to the highest continuous forests that we reached at both Wunaroahare (800 m) and Tsaraepae (700 m). The most common call was a series (~10+) of low, upwardly inflecting *woot* notes, spaced up to 2 sec apart. Infrequently, it also gave a soft, single *woot* note.

We found the Tanna Fruit Dove breeding at both sites. Bregulla (1992) reported its nesting status as poorly known, with previous evidence reported only in April and May, a time of little breeding activity among other landbirds in Vanuatu. At Wunaroahare, a nearly fledged nestling was found on the ground after a windy evening, and two males had enlarged testes and a female had enlarged ova. At Tsaraepae, the one bird collected was a female with enlarged ova.

*Ptilinopus greyii*.—The monotypic Red-bellied Fruit Dove is confined to New Caledonia, the Loyalty Islands, and Vanuatu. The species was abundant ( $\leq 50$ /day) at both sites in heavily disturbed to mature forests and at all elevations. It vocalized throughout the day. All specimens showed evidence of breeding: at Wunaroahare, these included a female with a ruptured follicle, another with enlarged ova, a male with enlarged testes, and a recently fledged juvenile; at Tsaraepae, the specimens included two males with enlarged testes, a female with enlarged ova, and two juveniles.

*Ducula bakeri*.—The monotypic Vanuatu Imperial Pigeon is endemic to seven islands in northern Vanuatu. Although rare or absent in the lowlands of Santo, it was common at Tsaraepae, where two or three calling individuals often were audible from many points on a forested ridge at ~600 m, and we recorded as many as 20 on single days. It was less common on the disturbed slopes below 500 m, although we heard it in a forest patch adjacent to Kerevalissy on 14 June. At Wunaroahare, we found the Vanuatu Imperial Pigeon only at elevations >800 m, where up to three individuals called in heavy forest cover on most days. The birds taken at Tsaraepae were an adult female with enlarged ova and a juvenile male. They differed little in plumage, and both had *Myristica* spp. fruits in their crops and stomachs.

*Chamosyna palmarum*.—The monotypic Palm Lorikeet is endemic to Vanuatu and the Santa Cruz Group. We recorded this species only twice (a flock of six on 8 June, a group of two on 11 June), both times in a *Ficus* spp. tree with large, fleshy fruits, in humid forest at 650 m on the main ridge at Tsaraepae. Although more characteristic of montane than lowland habitats, the Palm Lorikeet seems to undergo population fluctuations and has a propensity to wander (Medway and Marshall 1975, Bregulla 1992). Its preferred foods (flowers and fruits) may have been scarce at the time of our visits.

*Collocalia esculenta uropygialis* and *C. v. vanikorensis*.—Each of these widespread swiftlets was common at Tsaraepae. The Glossy Swiftlet (*C. esculenta uropygialis*; 20–

TABLE 3. Indigenous birds recorded (+ = present, - = not recorded) at six sites on Santo, Vanuatu, 2002–2003. English common names are provided for the species not included in Table 2. E = endemic to Vanuatu, e = endemic to Vanuatu plus New Caledonia and/or the Santa Cruz Group. Sources are Bowen (1997) for Loru Protected Area; Medway and Marshall (1975) for Apuna River, Hog Harbor, and Nokovula; and our own data for Wunaroahare and Tsarapae. For each site, the elevation (m) is included.

Species	Loru Protected Area 0–120 m	Apuna River 100 m	Hog Harbor 160 m	Wunaroahare 600–1,250 m	Tsarapae 500–700 m	Nokovula 1,120 m
<i>Megapodius layardi</i> (E)	+	+	–	–	+	–
<i>Falco peregrinus</i> , Peregrine Falcon	+	–	–	–	–	+
<i>Circus approximans</i>	+	+	–	+	+	+
<i>Gallirallus philippensis</i> , Banded Rail	+	–	–	–	–	–
<i>Columba vitiensis</i>	+	+	–	+	+	–
<i>Macropygia mackinlayi</i>	+	+	+	+	+	+
<i>Chalcophaps indica</i>	+	+	+	+	+	+
<i>Ptilinopus tannensis</i> (E)	+	+	–	+	+	–
<i>Ptilinopus greyii</i> (e)	+	+	+	+	+	+
<i>Ducula pacifica</i>	+	+	+	+	+	–
<i>Ducula bakeri</i> (E)	–	–	–	+	+	+
<i>Trichoglossus haematodus</i>	+	+	+	+	+	–
<i>Chamosyna palmarum</i> (e)	–	–	–	–	+	+
<i>Chrysococcyx lucidus</i>	–	–	–	+	+	–
<i>Tyto alba</i> , Barn Owl	+	–	–	–	–	–
<i>Collocalia esculenta uropygialis</i>	+	+	–	+	+	+
<i>Collocalia v. vanikorensis</i>	–	+	–	+	+	–
<i>Todiramphus farquhari</i> (E)	+	+	+	+	+	–
<i>Todiramphus chloris</i>	+	–	–	+	+	–
<i>Glycifohia n. notabilis</i> (E)	–	–	–	+	+	+
<i>Myzomela cardinalis</i>	–	+	+	+	+	+
<i>Gerygone flavolateralis</i>	–	+	–	+	+	+
<i>Artamus leucorhynchus</i>	+	–	–	+	+	+
<i>Coracina caledonica</i>	+	+	+	+	+	+
<i>Lalage maculosa</i>	–	–	–	+	+	–
<i>Lalage leucopyga</i>	–	–	–	+	–	+
<i>Pachycephala [pectoralis] caledonica</i> (e)	+	+	+	+	+	+
<i>Petroica multicolor ambrynsensis</i>	–	–	–	+	–	+
<i>Rhipidura [fuliginosa] albiscapa</i>	+	–	–	+	+	–
<i>Rhipidura spilodera</i>	+	+	+	+	+	+
<i>Neolalage banksiana</i> (E)	+	+	+	+	+	+
<i>Clytorhynchus pachycephaloides grise-scens</i> (e)	+	–	+	–	+	–
<i>Myiagra caledonica</i>	+	+	+	+	+	–
<i>Cichlornis whitneyi</i> , Melanesian Thick-etbird	–	–	–	–	–	+
<i>Zosterops flavifrons</i> (E)	+	+	+	+	+	+
<i>Zosterops lateralis</i>	+	–	–	+	+	+
<i>Alponis zelandica</i> , Rufous-winged Starling (e)	–	–	–	–	–	+
<i>Turdus poliocephalus vanikorensis</i>	–	+	+	+	–	+
<i>Erythrura cyaneovirens</i> , Red-headed Parrotfinch	–	–	–	–	–	+
Total species	25	22	16	30	30	24
Total endemic species (E + e)	8	8	6	8	11	8

50/day) generally flew much closer to the ground than the Uniform Swiftlet (*C. v. vanikorensis*;  $\leq 20$ /day, except for loose flocks of  $\sim 400$  that passed over on several mornings at Tsarapae, all flying west). Both species were

noted at all sites visited on Santo. Despite our careful observations of all swiftlets detected on Santo, we did not record the White-rumped Swiftlet (*Collocalia spodiopygia*), which was unknown to our guides.



TABLE 4. Avian specimen data from Santo, Vanuato, October–November 2002 and June 2003. Specimens collected at low elevations around Wusi and Kerevalissy villages and montane study sites are included. E = endemic to Vanuatu plus New Caledonia and/or the Santa Cruz Group. See Tables 2 and 3 for English common names. Juvenile status determined by presence of bursa of Fabricius, degree of skull ossification, condition of reproductive tract, and plumage. Breeding evidence (+ or –) determined on the basis of condition of reproductive tract, active nests, or recently fledged juveniles; NI = no information.

Species	Body mass (g) of specimens				Breeding evidence	
	Adult male	Adult female	Juvenile male	Juvenile female	Oct–Nov 2002	June 2003
<i>Gallirallus philippensis</i>	202, 210, 233, 244, 252	188, 252	222	156, 173	+	+
<i>Macropygia m. mackinlayi</i>	82	81, 82, 91, 94	70, 72	—	+	—
<i>Chalcophaps indica sandwicensis</i>	106, 117, 130, 134	100, 112, 118, 119	—	—	+	+
<i>Ptilinopus tannensis</i> (E)	202, 206	204, 221	91	—	+	+
<i>Ptilinopus greyii</i> (e)	86, 94, 95	65, 69, 88	83	73, 79	+	+
<i>Ducula p. pacifica</i>	515	—	—	—	NI	—
<i>Ducula bakeri</i> (E)	394	—	437	—	NI	+
<i>Trichoglossus haematodus massena</i>	118	102	—	—	NI	—
<i>Tyto alba</i>	—	301	—	—	—	NI
<i>Collocalia esculenta uropygialis</i>	4.8, 5.4, 5.4	4.9, 5.2, 5.9, 6.0	—	—	+	+
<i>Todiramphus farquhari</i> (E)	37, 39, 40.5	38, 39, 39.3	40	—	+	—
<i>Todiramphus chloris santoensis</i>	56.5	—	65	—	—	NI
<i>Glycyfobia n. notabilis</i> (E)	29.7	23.3, 26.4	—	26.4	+	—
<i>Myzomela cardinalis tenuis</i>	11.1, 11.9, 12.0, 12.1, 13.5	8.4, 9.7, 10.0	—	—	+	+
<i>Coracina caledonica thilenii</i>	159	—	155	—	—	NI
<i>Lalage maculosa modesta</i>	24.8	25.8	—	—	+	NI
<i>Pachycephala [pectoralis] caledonica intacta</i> (e)	23.3, 23.8, 26.0, 26.0, 26.2	23.2, 23.9	21.4, 23.3	23.0	+	+
<i>Petroica multicolor ambryensis</i>	8.4, 9.7	8.5	—	—	+	NI
<i>Rhipidura [fuliginosa] albiscapa brenchleyi</i>	8.1, 8.2, 8.4	7.1	7.8	—	+	+
<i>Rhipidura s. spilodera</i>	13.4, 13.4, 14.0	10.6, 11.0	—	11.4	+	—
<i>Neolalage banksiana</i> (E)	16.2, 17.9, 17.9, 18.0, 19.3, 20.2	15.5	18.1, 18.2	17.6	+	+
<i>Clytorhynchus pachycephalooides grisescens</i> (e)	25.0, 27.3, 28.0, 30.1	29.0	—	—	+	+
<i>Myiagra caledonica marinae</i>	12.8, 13.3, 14.6, 14.9, 15.7	12.1, 13.2	—	—	+	—
<i>Zosterops flavifrons brevicauda</i> (E)	10.2, 10.5, 10.9	10.0, 11.9	10.2, 10.3	9.9, 10.7, 11.0	+	+
<i>Zosterops lateralis tropicus</i>	13.3, 14.3	12.5, 13.2, 15.4	15.0	14.8	+	—
<i>Turdus poliocephalus vanikorensis</i>	42.5, 44.0, 46.0	46.0, 54	—	—	+	NI

*Todiramphus farquhari*.—Endemic to Santo, Malo, and Malakula, the Chestnut-bellied Kingfisher was slightly more common in the wet forests near Tsaraepae ( $\leq 5/\text{day}$ ) than in the dry forests of the western slope, although we recorded up to six daily at Wunaroahare. It was most common in high-canopy forests, but also persisted in forest patches, even near Kerevalissy village. It ranged from the lowlands up to at least 800 m, overlapping the entire elevational range of its larger congener, the Collared Kingfisher (*T. chloris*), which prefers more open habitat. The Chestnut-bellied Kingfisher was very vocal at both sites, often singing throughout the day. The call is a series of ascending notes with decreasing intervals, not the “monotonous single note” described by Bowen (1997). The two birds collected at Wunaroahare, both at 600 m, were adult males, one in non-reproductive condition (testes  $3 \times 1.5$  mm) and the other with somewhat enlarged testes ( $6 \times 4$  mm). Evidence of reproductive activity at Tsaraepae included a juvenile male (probably in first pre-basic molt, with heavy wing molt and moderate body molt), and two adult females with convoluted oviducts but unenlarged ova. Stomachs contained the remains of large beetles (including Cerambycidae), large orthopterans, spiders, skinks, and geckos.

*Glycifohia notabilis*.—The monotypic White-bellied Honeyeater is endemic to Santo and Malakula. With Dickinson’s (2003) placement of this species in the genus *Glycifohia* (previously classified as *Phylidonyris*), its only congener—the Banded Honeyeater (*G. undulata*)—is endemic to New Caledonia. Previously, both had been placed in the widespread Australian genus, *Phylidonyris*. The White-bellied Honeyeater occurred in similar abundance between 600 and 800 m at both sites, usually in large tracts of forest. Often, these birds congregated at flowering trees in noisy groups of  $\leq 15$  individuals. Of four specimens (two from each site), only one was reproductively active, a male from Wunaroahare with enlarged testes. The other bird from this site, an adult female (no bursa; skull 100% ossified), had minute ova, a straight oviduct (probably had not yet bred), and its wings, tail, and body were molting. An adult female from Tsaraepae had these same characteristics. A young male (bursa  $2 \times 2$  mm)

from Tsaraepae also was molting, probably its first pre-basic molt.

*Petroica multicolor ambrynnensis*.—The subspecies of Pacific Robin from Santo, *P. m. ambrynnensis*, is one of 5 subspecies from Vanuatu and 14 across Oceania. In the Solomons and New Guinea, the Pacific Robin is restricted to montane forests. Although apparently restricted to high-elevation forests ( $> 500$  m) on Santo, the Pacific Robin may be found at lower elevations elsewhere in Vanuatu. JJK found it to be common in lowland forests on the rain-shadowed Dillon’s Bay area of western Erromango. On Efate, however, DWS found it in humid, mid-elevation forest ( $\sim 350$  m). In addition to not finding the Pacific Robin at Tsaraepae (although our guides there knew of this species), no one has recorded it from any lowland location on the wet (eastern) side of Santo. Medway and Marshall (1975) recorded it at an elevation of 1,100 m on the eastern flank of Mt. Tabwemasana, but we recorded robins (up to four daily) only in forest from 650 to 800 m near Wunaroahare. The three specimens were two adult males with enlarged testes and seminal vesicles, and an adult female that probably had nested recently (ova not enlarged, but oviduct somewhat thickened and convoluted).

*Neolalage banksiana*.—The Buff-bellied Monarch belongs to a monotypic genus endemic to Vanuatu. It occurs on most major islands south to Efate and was common at both of our primary study sites, with daily records of up to 25 at Wunaroahare and 12 at Tsaraepae. It was found most often in pairs or family groups in the undergrowth of forest patches or large tracts of forest, especially where vine tangles or thickets of *Hibiscus tiliaceus* dominate the understory, although some birds were found in forests with an open understory.

The song of the Buff-bellied Monarch is apparently undescribed; Bregulla (1992) stated that, “. . . it is said to have melodious song.” AWK tape-recorded a bird singing in scrubby dry forest adjacent to Wusi village on the morning of 25 October. The song had a stuttering, jumbled beginning, then three rapid series of reedy, high-pitched, whistled notes. The first and last series consisted of three descending notes, whereas the second series consisted of only two descending notes: *tee-*

*dee-dee—tee-dee—tee-dee-deee*. The song, which lasts ~3 sec, resembled that of the Fantailed Gerygone (*Gerygone flavolateralis*) but was shorter, and the tone of the notes was more pure. The call note (a drawn-out, single burry note that increased in amplitude) was given between songs. The song was heard (infrequently) in montane forests at Wunaroahare as well, but not at Tsaraepae the following June. Nevertheless, Buff-bellied Monarchs called frequently throughout the day at both sites, especially pairs that called to one another while foraging.

Breeding activity of this species was pronounced at Wunaroahare, where a near-finished nest was discovered on 1 November, 2.5 m above ground in the fork of a sapling in humid forest. The nest was similar to those described for the species by Bregulla (1992) and Bowen (1997). At least two pairs of Buff-bellied Monarchs were found accompanied by recently fledged young at Wunaroahare. Two of the three adult males taken at Wunaroahare had enlarged testes; the other male had somewhat enlarged testes, whereas the female lacked a bursa but had a straight oviduct, indicating that she had not bred previously. At Tsaraepae, one of the two adult male specimens had enlarged testes. The other three specimens from Tsaraepae were young birds with bursae and incompletely ossified skulls. The plumage of adult males is slightly more vividly colored than that of adult females or non-adults.

*Clytorhynchus pachycephaloides griseescens*.—The inconspicuous Southern Shrikebill species is found only in New Caledonia and Vanuatu. The subspecies *C. p. griseescens* is endemic to Vanuatu. Once we learned its vocalizations (see below), we recorded  $\leq 4$ /day in dense forest at Tsaraepae (600–650 m). Although we netted four (in 165 net-hr) in dry forest near sea level at Wusi village, we neither netted (in 337 net-hr) nor recorded any in the higher-elevation forests at Wunaroahare. One also was seen by AWK at the Vatte Conservation Area in northern Santo in November 2002, and the species was heard often and seen occasionally in lowland forests at the Loru Protected Area (Bowen 1997). Shrikebills were netted rarely (0.006/net-hr) at two lowland forest sites east of the main cordillera by Medway and Marshall (1975), although

none was found at their higher-elevation site (1,120 m). The birds we observed were sluggish, perching from near the ground to 8 m above ground in the humid forest.

Bregulla (1992) described the Southern Shrikebill's song as highly variable "drawn out whistled sounds in cadence." On 10 June at Tsaraepae, AWK tape-recorded a three-part song made up of two evenly spaced, harsh *chek* notes, followed by a descending, drawn-out, burry whistle. The most commonly recorded call was a single, burry musical note, similar to that of the Buff-bellied Monarch, but less raspy and dropping in pitch at the end.

Testes of the male collected at Tsaraepae were somewhat enlarged (10 × 5 mm), indicating recent reproductive activity. The four taken near sea level at Wusi were adults (no bursae, skull 100% ossified) consisting of two reproductively active males (testes enlarged) and a nonbreeding male and female.

*Zosterops flavifrons*.—Endemic to Vanuatu, the Yellow-fronted White-eye was one of the most common forest birds at both sites, as it is throughout much of the archipelago (AWK, JJK, DWS pers. obs.). Up to 75 were found daily from near sea level to the highest elevations that we visited (1,250 m at Wunaroahare, 700 m at Tsaraepae). We often found White-eyes in fruiting trees, where flocks of  $\leq 15$  kept up a persistent chatter. It co-occurred at some forest edges with a larger congener (*Z. lateralis*, the Silver-eye), although the latter usually was absent from the large tracts of mature forest where the Yellow-fronted White-eye was most common. At Wunaroahare, all adult specimens were in reproductive condition (three males, two females). At Tsaraepae, all five specimens were young birds (with bursae and/or incompletely ossified skulls): two were undergoing wing molt, three were in tail molt, and all were undergoing body molt.

*Turdus poliocephalus vanikorensis*.—The extremely polytypic Island Thrush (51 recognized subspecies; Dickinson 2003) occurs irregularly from the Philippines to Samoa. Among the eight subspecies occurring in Vanuatu is *T. p. vanikorensis*, found on Santo, Malo, and the Santa Cruz Group. Similar to the Pacific Robin, today the Island Thrush is restricted to montane forests on some islands (e.g., New Guinea, New Ireland), whereas on



others (e.g., Rennell in the Solomon Islands) it lives in the lowlands. Fossils from coastal sites in Tonga (where it no longer occurs) and New Ireland indicate that the Island Thrush has undergone considerable range contraction since the arrival of humans on the islands (Steadman 1993, 2006b).

The Island Thrush was absent at Tsaraepae but common at Wunaroahare, where we found it in dry forests near sea level (0.03/net-hr), in montane forests at 600–800 m in elevation (0.03/net-hr), and in forest patches at 1,250 m (0.08/net hr). Birds collected near Wusi included adults of both sexes with enlarged gonads. The current distribution of the Island Thrush on Santo resembles that of the Pacific Robin in being present in dry forest on the western slopes of the cordillera but absent (or very rare) in humid forests to the east. Likewise, Bowen (1997) did not record it at the Loru Protected Area. This may reflect a recent change in its status east of the cordillera, where the Island Thrush was recorded frequently at two lowland forest sites in 1971 (Hog Harbour, Apuna River; Medway and Marshall 1975). Predation by feral cats may be the cause of the apparent decline of the Island Thrush on Santo.

## DISCUSSION

*Inter-site (intra-island) comparisons.*—Of the 39 species of landbirds recorded from at least one of the six surveyed sites on Santo (Fig. 1, Table 3), only 17 (44%) were found at five or six sites. These included 5 of the 11 endemic or near-endemic species. Three species known from Santo (*Gallicolumba sanctaerucis*, *Cacomantis pyrrhophanus*, *Aplonis santovestris*) were not recorded at any of the sites. That more species are not more widespread on Santo may be due to elevational factors; nine species are known only from one or more of the three highland (>500 m) sites (*Aplonis santovestris* also is restricted to highlands), and two species (*Gallirallus philippensis*, *Tyto alba*) are recorded only from lowland sites (<500 m). Of the remaining species found at fewer than five sites, some preferred more open habitats (*Todiramphus chloris*, *Rhipidura albiscapa*, *Artamus leucorhynchus*, *Zosterops lateralis*) and some were rare (*Megapodius lyardi*, *Falco peregrinus*, *Gallicolumba sanctaerucis*, *Charmosyna palma-*

*rum*, *Aplonis zelandica*); for unknown reasons, others (*Columba vitiensis*, *Ptilinopus tannensis*, *Cacomantis pyrrhophanus*, *Collocalia vanikorensis*, *Turdus poliocephalus*) occur only locally.

The inter-site variation in landbird communities on Santo is noteworthy. In island biogeography, it has been common practice to assemble lists based on the entire fauna or flora of an island, even though many species may rarely, if ever, interact because they are not syntopic. Because much of island biogeography theory (e.g., MacArthur and Wilson 1967; Diamond and Marshall 1977; Diamond 1980, 1982; Mayr and Diamond 2001) is based on analyses at the community level, it may be more biologically informative to compare the avifauna from single sites, rather than the entire avifauna of islands, especially on large islands where strong elevational and precipitation gradients occur (e.g., Santo). Aside from the massive island of New Guinea, there is no island in Melanesia for which bird survey data have been published for as many sites as those on Santo. We urge biologists working on islands to undertake the surveys needed to generate data on presence/absence, relative abundance, and habitat preference of birds from single sites.

*Inter-archipelago comparisons.*—Compared with a forested lowland site on the similarly sized island of Isabel (3,995 km<sup>2</sup>; Fig. 1) in the Solomon Islands (Kratter et al. 2001a, 2001b), the species richness at the sites on Santo was much lower (25–30 versus 59 resident species of forest birds). Pigeons and doves contributed equally to richness (seven species at sites on either island), whereas passerine diversity was not as rich on Santo but contributed a higher percentage to species richness (15–16 species or 50–53% at the Santo sites, versus 21 species or 36% at Isabel). The sites on Santo also had markedly fewer hawks and falcons (one compared with five species on Isabel), parrots (two versus six species), and kingfishers (two versus six species). In addition, the sites on Santo held a smaller portion of the entire forest bird avifauna than that found along the Garanga River on Isabel: the 30 species found at either Wunaroahare or Tsaraepae represent 71% of the 42 species known from Santo, whereas the 59 species found along the Garanga River rep-



resent 84% of the 70 species of landbirds known from Isabel. This may have been due, in part, to our longer stay at the Garanga River site (21 days over 2 years versus 6 and 7 days at Wunaroahhare and Tsaraepae, respectively). Another possible factor is that, for a given island in Oceania, lowland forests tend to support richer bird communities than montane forests (Mayr and Diamond 2001).

*Species not recorded at our sites.*—At Wunaroahhare and Tsaraepae, we failed to record seven species known to occur in forests on Santo—the Peregrine Falcon (*Falco peregrinus*), Santa Cruz Ground Dove (*Gallicolumba sanctaerucis*), Fan-tailed Cuckoo (*Cacomantis pyrrhophanus*), Rufous-winged Starling (*Aplonis zelandicus*), Mountain Starling (*A. santovestris*), Melanesian Thicketbird (*Cichlornis whitneyi*), and Red-headed Parrotfinch (*Erythrura cyaneovirens*). Our guides knew the Peregrine Falcon and called it “vusavusa” in the Hakei language; it may be a rare resident at or near our sites, most likely in areas with cliffs. The Santa Cruz Ground Dove is considered rare in montane forests (Bregulla 1992); our guides, however, knew it and called it “nono.” Perhaps restricted to the lowlands, the Fan-tailed Cuckoo has become rare in Vanuatu (Bregulla 1992), and our guides did not recognize it. The Fan-tailed Cuckoo also was not recorded at the other four sites surveyed in 1971 and 1995 (Medway and Marshall 1975, Bowen 1997), although Bregulla (1992) considered it uncommon on Santo.

The Mountain Starling is known to occur only in cloud forest at elevations >1,150 m on Santo (Medway and Marshall 1975), and, on the southern slopes of Peak Santo, the starling was not found below 1,400 m (Bregulla 1992). The Rufous-winged Starling is thought to be common in forests at around 1,000 m on Santo (Bregulla 1992). Although it could be absent from the drier forests on the western slope, we suspect that we would have found it on the wetter southern slopes had the rainfall diminished, thereby allowing us access to higher elevations. Our guides did not recognize the illustrations (in Bregulla 1992) of either starling species. The Melanesian Thicketbird is a streamside specialist, and we did not sample streamside at either site. Our guides knew the species, however, explaining

that it lives close to the ground along high-elevation streams; they called the male “sisi-va” and the female “sisiriva.” The Red-headed Parrotfinch (*Erythrura cyaneovirens*) is an uncommon fig specialist suspected of being nomadic, which likely explains its absence from seemingly suitable habitats if the large, fleshy fig fruits that it prefers (Bregulla 1992; DWS pers. obs. on Efate Island, 3 August 1997) are scarce or absent. Our guides had no name for Red-headed Parrotfinch.

Finally, bones from archaeological sites elsewhere in Vanuatu give clues about which species once may have lived on Santo. DWS and JJK have identified extinct or extirpated species of megapode (*Megapodius* undescribed sp.) and hawk (*Accipiter* cf. *fasciatus*) on Efate, flightless rail (*Porzana* undescribed sp.) and parrot (*Eclectus infectus*; Steadman 2006a) on Malakula, and starling (*Aplonis* undescribed sp.) on Erromango. Given that most volant species of Pacific Island landbirds were more widespread before the arrival of humans on the islands (Steadman 1995, 2006b), we suspect that these (or similar species in the case of flightless rails) once lived on Santo and many other islands in Vanuatu.

#### ACKNOWLEDGMENTS

We kindly thank D. Kalfatak and E. Bani of the Vanuatu Environment Unit for permission to undertake this research, and for logistical assistance. We are very grateful to R. Regenvanu and the staff of the Vanuatu National Museum for crucial logistical support and advice. For assistance at our field sites we thank K. Alvea, Chief Bua and the residents of Wusi, W. Dauron, M. K. Hart, R. Kolomule, Chief P. Leon and the residents of Kerevalissy, S. Nisak, R. Palo, and P. Tavouiruja. Funding (to DWS) was provided by the University of Florida Division of Sponsored Research (Research Opportunity Fund grant U001) and National Science Foundation grant EAR-9714819. We thank G. Dutton and two anonymous reviewers for constructive comments on the manuscript.

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